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ORIGINAL PAPER

Life strategy and diet of *Calanus glacialis* during the winter–spring transition in Amundsen Gulf, south-eastern Beaufort Sea

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Abstract The copepod *Calanus glacialis* plays a key role in the lipid-based energy flux in Arctic shelf seas. By utilizing both ice algae and phytoplankton, this species is able to extend its growth season considerably in these seasonally ice-covered seas. This study investigated the impacts of the variability in timing and extent of the ice algal bloom on the reproduction and population success of *C. glacialis*. The vertical distribution, reproduction, amount of storage lipids, stable isotopes, fatty acid and fatty alcohol composition of *C. glacialis* were assessed during the Circumpolar Flaw Lead System Study. Data were collected in the Amundsen Gulf, south-eastern Beaufort Sea, from January to July 2008 with the core-sampling from March to April. The reduction in sea ice thickness and coverage observed in the Amundsen Gulf in 2007 and 2008 affected the life strategy and reproduction of *C. glacialis*. Developmental stages CIII and CIV dominated the overwintering population, which resulted in the presence of very few CV and females during spring 2008. Spawning began at the peak of the ice algal bloom that preceded the precocious May ice break-up. Although the main recruitment may have occurred later in the season, low abundance of females combined with a potential mismatch between egg production/development to the first feeding stage and phytoplankton bloom resulted in low recruitment of *C. glacialis* in the early summer of 2008.

Keywords *Calanus glacialis* · Life cycle · Reproduction · Ice algae · Fatty acid composition · Amundsen Gulf

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Introduction

Calanus glacialis Jaschnov is an Arctic shelf copepod species with circumpolar distribution. It is abundant in the northern Barents Sea, along the east and west Greenland shelf, the Baffin Bay, through the Canadian Archipelago, along the north-west coast of North America, and the Siberian shelf and the White Sea (Jaschnov 1970; Hirche and Kwasniewski 1997). *C. glacialis* together with *C. hyperboreus* Krøyer make up >70% of the zooplankton biomass in the south-eastern Beaufort Sea (Darnis et al.

2008). *C. glacialis* has a 1- to 3-year lifespan, depending on the environment (Tande 1991; Falk-Petersen et al. 2007). It undertakes marked seasonal migration. In autumn, it descends to depth and overwinters in a state of dormancy (diapause) and ascending to the surface to feed and reproduce the following spring (Kosobokova 1999).

As light increases during the winter–spring transition at high latitudes, it triggers the short and intense bloom of ice algae (Różańska et al. 2009), and the phytoplankton bloom that follows ice break-up (Zenkevitch 1963; Falk-Petersen et al. 2009). The carbon fixed through these two blooms is rapidly converted into lipid reserves or reproductive output by the *Calanus* species (Sargent and Henderson 1986; Falk-Petersen et al. 2000; Lee et al. 2006). *C. glacialis* stores energy in the form of neutral lipids (mainly wax esters) that are vital energy sources during overwintering and reproduction (Lee et al. 2006), although spawning success seems to be related to additional input from either fresh ice algae or phytoplankton (Niehoff et al. 2002; Søreide et al. 2010). This copepod can spawn as early as March/April and as late as August/September, depending on the sea ice conditions that largely determine the onset of the algal growth season (Hirche 1989; Søreide et al. 2008).

The fatty acid trophic marker (FATM) and stable isotope methods provide information on trophic position, diet and energy transfer. The stable nitrogen values give a good estimate of trophic level since the consumers are typically enriched in δ^{15}N by 3–4% relative to their diet (Søreide et al. 2006b), whereas the fatty acid composition provides more detailed information on what the consumers have been eating (Dalsgaard et al. 2003). *C. glacialis* incorporates dietary fatty acids, particularly polyunsaturated fatty acids (PUFAs), relatively unchanged into their lipid reserves, making it possible to trace lipid energy pathways through the marine food web. The long-chain PUFAs 20:5n3 (eicosapentaenoic acid, EPA) and 22:6n3 (docosahexaenoic acid, DHA) are omega-3 fatty acids that are exclusively produced by marine algae and are essential for reproduction and growth of all marine organisms (Ackman 1989). *Calanus* spp. is a key organism in transferring these PUFAs from primary producers to higher trophic levels (Falk-Petersen et al. 2009). Diatoms are characterized by high proportions of the monounsaturated fatty acid (MUFA), 16:1n7, C16PUFAs and EPA, whereas species of *Phaeocystis* Lagerheim and dinoflagellates contain high proportions of the C18 PUFAs and DHA (Dalsgaard et al. 2003). High proportions of these PUFAs in copepods indicate herbivorous feeding (Dalsgaard et al. 2003). However, the FATM technique can only determine trophic relationships qualitatively.

The Arctic Ocean and its peripheral seas have had a succession of record-breaking low sea ice coverage in the last decade (NSIDC 2011), including in the CFL study area (Barber et al. 2010). The dramatic reduction in sea ice extent and thickness (Rothrock et al. 2008) may alter the functioning of the Arctic marine ecosystem. For instance, a shorter ice algal growth season and a subsequent earlier onset of the spring phytoplankton bloom are expected. In this context, the aim of our investigation was to study *C. glacialis* population dynamics during a time of changing ice conditions. To do so, we investigated vertical distribution, egg production, lipid biochemistry and diet of *C. glacialis* during the winter–spring transition of the low sea ice year of 2008 in the Amundsen Gulf, south-eastern Beaufort Sea.

This study, which was part of the Circumpolar Flaw Lead Study (CFL), involved the overwintering of CCGS *Amundsen* in the Beaufort Sea during the International Polar Year (IPY) 2007-2008. It was also a component of a pan-Arctic study aimed to compare the ecology of *C. glacialis* from different Arctic regions to increase our knowledge of this important shelf species.

Materials and methods

Study area

The Amundsen Gulf (60,000 km^2) bridges the Beaufort Sea to the Canadian Arctic Archipelago (Fig. 1). The surface water in the region comprises the Pacific Ocean, while the deeper water below 200 m originates from the Atlantic Ocean (Carmack and MacDonald 2002). The basic surface circulation is dominated by the anticyclonic Beaufort Sea Gyre that entrains the pack ice and surface waters westward towards the Canada Basin, while, below 80 m depth, the cyclonic Beaufort Undercurrent carries waters of both Pacific and Atlantic origin eastward along the continental margin and into the Amundsen Gulf (Ingram et al. 2008). Seasonal sea ice begins to form in October at the coastal boundaries of the gulf, and by late December, the ice consolidates over the entire region. In early April, a land-fast ice bridge typically forms south of Banks Island to the continent. By May–June, break-up begins and the flaw lead polynya enlarges to form the Cape Bathurst polynya complex at the entrance of Amundsen Gulf. Satellite data indicate large inter-annual variability in the extent and persistence of open water regions (Arrigo and van Dijken 2004). During our study year, the ice did not consolidate over the entire region, nor did the land-fast ice bridge form.

Sampling of *Calanus*

Sampling for the assessment of *Calanus glacialis* vertical distribution, lipid composition and stable isotopes was carried out from the CCGS *Amundsen* between January and

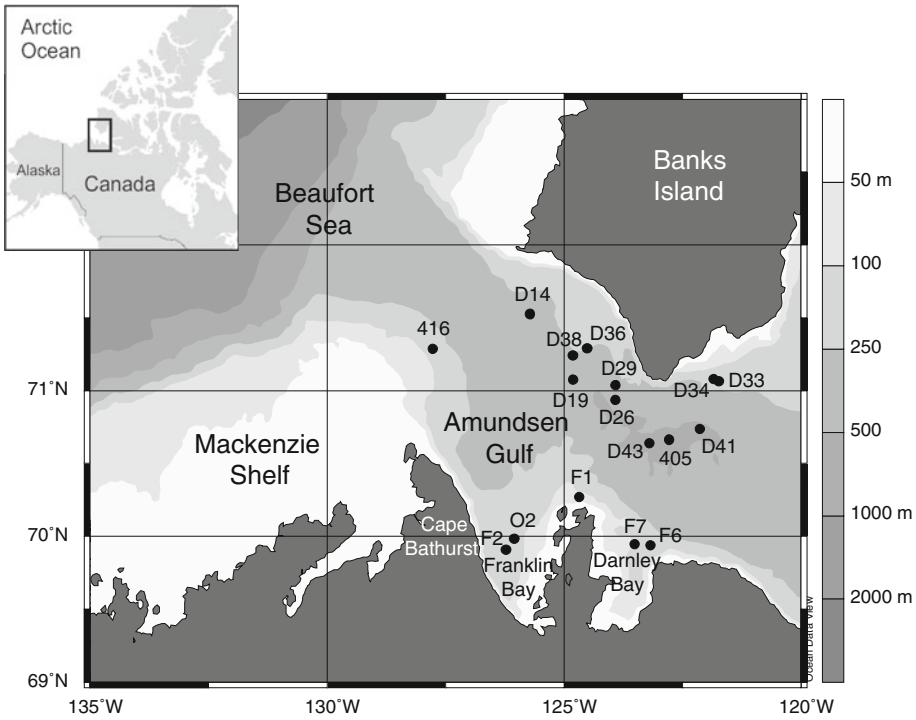

Fig. 1 Sampling stations in Amundsen Gulf, south-eastern Beaufort Sea, where zooplankton and ice algae were collected from January to July 2008, during the circumpolar flaw lead (CFL) system study field programme onboard the CCGS *Amundsen*

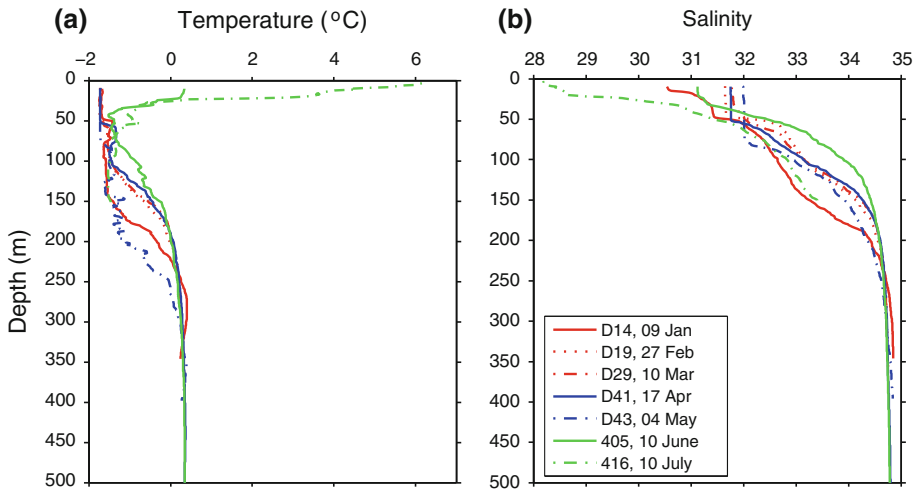

Fig. 2 Temperature and salinity at the sampling stations in the Amundsen Gulf from January to July 2008

July 2008 during the CFL field programme in the Amundsen Gulf (121°46′–124°38′ W, 70°47′–71°18′N; Fig. 1). Samples were taken within two main areas: Amundsen Gulf polynya hereafter referred to as Amundsen Gulf (average depth 360 m) and the shelf of Franklin Bay and Darnley Bay (average depth 150 m). Our aim of overwintering with the CCGS *Amundsen* was to conduct repeated sampling at one location in the Amundsen Gulf. Due to unusual winter 2008 ice conditions, and the moving ice and open leads (Barber et al. 2010), the ship had to relocate many times, resulting in a wider sampling area than initially planned. Nevertheless, the sampling sites in this study were within the area where Darnis et al. (2008) characterized the polynya assemblage of zooplankton. The temperature and salinity from the sampled stations (Fig. 2) show seasonal differences among stations due to sea ice melting and warming.

The vertical distribution of *C. glacialis* was determined using a Hydro-Bios Multi Plankton Sampler type midi (200-µm mesh, opening 0.50 m^2, 9 distinct depths) that was deployed from the ship's moonpool. The sampler was hauled vertically from 10 m above the sea floor to the surface at a speed of 30 m min^{-1}. The nine depth layers sampled were 0–20, 20–40, 40–60 m, three strata of 20 m depth starting 10 m above the bottom, and three intermediate layers between top and bottom that were equal and dependent on the depth of the water column (Table 1). Samples for taxonomic analysis were preserved with a 4%

Table 1 Summary of ice algae and *Calanus glacialis* samples collected in the Amundsen Gulf (AG), Franklin Bay (FB) and Darnley Bay (DB) from January to July 2008

Parameter	Station	Area	Date	B. depth (m)	Sample depth (m)	Sample type	Stage
Ice algae	D29	AG	17 and 18 March	401	Ice core	Taxonomy; Chl *a*	
	D33	AG	28 March and 03 April	187	Ice core	Taxonomy; Chl *a*	
	D36	AG	06 April	187	Ice core	Taxonomy; Chl *a*; FA of TL	
	D38	AG	11 April	269	Ice core	FA of TL	
	D41	AG	16 and 19 April	503	Ice core	Taxonomy; Chl a; FA of TL	
	D43	AG	26 and 29 April	554	Ice core	Chl *a;* FA of TL	
	D43	AG	05 May	404	Ice core	Chl *a*	
	F1	FB	08 May	55	Ice core	Taxonomy; Chl *a*; FA of TL	
	F2	FB	16 May	192	Ice core	FA of TL; Chl *a*	
Calanus glacialis							
Abundance	D14	AG	09 January	360	345-325-305-285-210-135-60-40-20-0		
	D19	AG	04 February	346	325-305-285-265-195-125-60-40-20-0		
	D29	AG	10 March	321	300-280-260-240-180-120-60-40-20-0		
	D41	AG	17 April	541	525-505-480-465-330-195-60-40-20-0		
	D43	AG	04 May	407	380-360-340-320-230-145-60-40-20-0		
	405	AG	10 June	573	560-540-520-500-350-200-60-40-20-0		
	405	AG	21 July	592	580-560-540-520-360-200-60-40-20-0		
	02	FB	12 May	190	185-165-145-125-100-80-60-40-20-0		
	F6	DB	16 June	205	190-170-150-130-105-80-60-40-20-0		
Lipids	D19	AG	02 February	346	Bottom-0	FA + FAOH of NL	Females
	D26	AG	27 February	377	Bottom-0	FA + FAOH of NL; FA of PL	Females
	D29	AG	12 March	315	Bottom-0	FA + FAOH of NL	Females
	D33	AG	24, 25 and 26 March	187	Bottom-0; 170-100 and 50-0	FA + FAOH of NL; FA of PL	Females; CIV
	D36	AG	06 and 08 April	302	270-200 and 50-0	FA + FAOH of NL; FA of PL	Females; CIV
	D41	AG	15 and 16 April	541	450-200 and 50-0	FA + FAOH of NL; FA of PL	Females; CIV
	02	FB	11 May	204	Bottom-0	FA + FAOH of NL	Females
	F6	DB	03 June	70	Bottom-0	FA + FAOH of NL; FA of PL	Females
	F7	DB	21 June	104	Bottom-0	FA + FAOH of NL	Females
	416	AG	10 July	157	Bottom-0	FA + FAOH of NL; FA of PL	Females
	D34	AG	13 July	182	Bottom-0	FA + FAOH of NL; Fa of PL	Females; CV

Table 1 continued

Parameter	Station	Area	Date	B. depth (m)	Sample depth (m)	Sample type	Stage
Stable isotopes	D29	AG	16 March	401	300-380 and 50-0	Stable isotope	Females
	D33	AG	01 April	187	50-0	Stable isotope	Females; CIV
	D36	AG	08 April	302	50-0	Stable isotope	Females; CIV
Egg production	D29	AG	18 March	401	50-0	24-h incubation	
	D33	AG	24–27 March and 1–3 April	187	50-0	3-day incubation	
	D36	AG	8–11 April and 12–15 April	187	50-0	3-day incubation	
	D41	AG	16 April	503	50-0	24-h incubation	
	D43	AG	26 April and 2 May	554	50-0	24-h incubation	
	405	AG	19 May	520	50-0	24-h incubation	
	02	FB	11 May	204	50-0	24-h incubation	

FA fatty acids, *TL* total lipid, *FAOH* fatty alcohols, *NL* neutral lipid, *PL* polar lipid

buffered seawater formaldehyde solution just after sampling.

For lipid analyses, *C. glacialis* females from the entire water column were collected monthly between January and July 2008 from the ship's moonpool with a large ring net (1-m^2 square metal frame and 200-µm mesh size; Table 1). From 16 March to 16 April, additional females and CIV were sampled weekly, for lipid and stable isotope analyses, from the ship's moonpool at two different depths: surface layer (0–50 m) and bottom layer (>150 m) using the Hydro-Bios sampler (Table 1). Animals were kept in the dark at in situ temperature and sorted as soon as possible after sampling. The largest stages of *C. glacialis* were identified according to their morphology and their prosome length by use of a stereomicroscope (Leica MZ6) and frozen immediately at –80°C for later stable isotope and lipid analyses (see below).

Ice algae

Ice algal samples were collected from 16 March to 5 May in Amundsen Gulf, and on 8 and 16 May in Franklin Bay (Table 1). Triplicate bottom ice cores were collected using a 9-cm-diameter Mark II coring system (Kovacs Enterprises) and kept in isothermal containers until further processing onboard the ship. The bottom 3 cm of each ice core was sampled for algal taxonomy, chlorophyll (chl *a*) and fatty acid composition.

In the ship's laboratory, ice core sections were melted in 0.2-µm filtered seawater to obtain a 3:1 dilution ratio to avoid osmotic shock (Garrison and Buck 1986). Duplicate subsamples were then filtered through GF/F filters for chl *a* determination. After at least 18 h extraction in 10 ml of 90% acetone at 5°C in the dark, chl *a* was measured using a Turner Designs 10-AU fluorometer, before and after acidification with 5% HCl. Volumes filtered ranged from 2 to 100 ml depending on sea ice algal biomass.

Cells ≥4 µm were identified to the lowest possible taxonomic rank and enumerated under an inverted microscope (WILD Heerbrugg) fitted with phase-contrast optics (Lund et al. 1958). During the bloom period, a minimum of 400 cells were counted in each settling chamber, except for samples in March, when 200–300 cells were counted due to very low abundance of cells.

For fatty acid analyses, defined volumes (40–120 ml) of thawed samples were filtered through pre-combusted (3 h, 500°C) 25-mm GF/F filters and immediately stored at −80°C. Total lipid was extracted in 15 ml chloroform/methanol (2:1, v:v; Folch et al. 1957). A known amount of heneicosanoic acid (21:0) was added as internal standard, and an acid-catalysed transesterification was carried out with 1% sulphuric acid in methanol (Christie 1982). The extract was cleaned using a silica column, and the composition of the fatty acid methyl ester was determined by gas chromatography (GC-FID; Leu et al. 2006). Individual components were identified and quantified using a ChemStation software package (Agilent). Fatty acids are presented as mass percentages of total fatty acids.

Zooplankton analyses

Community analyses

Zooplankton samples for community analyses were sieved through 150- and 1,000-µm sieves. The two size fractions (200–1,000 and >1,000 µm) were resuspended in filtered

Table 2 Dominant ice diatom species (%) in the Amundsen Gulf (AG, March–April) and Franklin Bay (FB, May) in 2008

Date	18 March	28 March	03 April	06 April	16 April	08 May
Station	D29	D33	D33	D36	D41	F1
Area	AG	AG	AG	AG	AG	FB
Cylindrotheca closterium (Ehrenberg) Reimann and Lewin	3.9	2.0	0.8	1.0	0.4	–
Fragilariopsis cylindrus (Grunow ex Cleve) Frenguelli	8.9	2.6	15.0	6.2	8.6	–
Navicula directa (W. Smith) Ralfs	0.7	2.8	2.9	–	–	0.4
Navicula pelagica Cleve	4.3	39.1	33.9	32.1	9.5	27.7
Navicula septentrionalis (Grunow) Gran	1.1	0.3	2.6	14.5	13.8	2.2
Nitzschia frigida (Grunow) Cleve	22.9	5.4	5.0	20.5	27.5	40.4
Nitzschia promare Medlin	2.1	–	2.1	2.8	15.8	–
Pauliella taeniata (Grunow) Round and Basson	–	–	–	–	–	2.9

seawater, and all the copepods in a known aliquot containing approximately 300 animals were identified to species level under a stereomicroscope. Young developmental stages of *C. glacialis* and the congener *C. hyperboreus* were separated according to differences in prosome length established during a previous overwintering expedition in the south-eastern Beaufort Sea (Canadian Arctic Beaufort shelf Exchange Study 2003–2004, see Table 2 in Forest et al. 2011). In our study area, the Pacific sub-Arctic *Calanus marshallae* Frost may be present (Frost 1974), and if that was the case, these copepods were pooled with *C. glacialis* due to difficulties in separating these two sibling species. Biomass (g DW m^{-2}) of *C. glacialis* was calculated, using the conversion factor (mg DW ind^{-1}) for each stage from Karnovsky et al. (2003).

Egg production

For egg production measurements, *C. glacialis* females were collected from the surface waters (0–50 m), with a ring net deployed from the ice, and gently sorted directly after capture by use of a truncated pipette. Twenty females were put in separate egg production chambers of 120 ml each equipped with 1,000-µm mesh false bottoms to avoid egg cannibalism and incubated for 3 days. The chambers were filled with 45 ml of 60-µm filtered seawater, collected from the same depth as the females, which was changed every day. For females incubated for 24 h, 30 animals were individually placed in a 30-ml petri dish, fitted with a false bottom (333-µm mesh) to prevent egg cannibalism. The petri dishes were filled with filtered (0.7 µm) seawater. All females were incubated at in situ temperature (approximately 0°C) in the dark. For the 3-day incubations, eggs and faecal pellets were counted every day.

Lipid and stable isotope analyses

Lipids of *C. glacialis* collected in the surface and at depth were analysed at Unilab in Tromsø, Norway, whereas lipids of *C. glacialis* collected from the whole water column were analysed at the Alfred-Wegener-Institute (AWI) in Bremerhaven, Germany. In both laboratories, total lipids were extracted according to Folch et al. (1957) and then separated into polar (PL) and neutral lipids (NL). Unilab used the separation method according to Graeve and Janssen (Graeve and Janssen 2009) using a HPLC 1200 (Agilent) equipped with a chromolith-performance Si column (Merck) and a fraction collector. At AWI, lipids were separated by column chromatography using a small glass column filled with silica gel 60H. Neutral lipids were eluted with hexane/diethylether (80:20, v:v) and polar lipids with a mixture of methanol/dichloromethane (80:20, v:v). Fatty acid methyl ester and free alcohols were then simultaneously analysed with a gas liquid chromatograph (HP 6890 N) on a 30 m, 0.25 mm i.d. wall-coated open tubular liquid phase column, equipped with split/splitless injector (250°C) and flame ionization detector (280°C) with an oven thermal gradient from an initial temperature of 60–150°C at 30°C min^{-1}, and then to a final temperature of 230°C at 1.5°C min^{-1}.

At AWI, the fatty acids and fatty alcohols were quantified with a 23:0 fatty acid methyl ester as internal standard, added to the sample before the total lipid extraction. Individual components were identified by comparisons with standards or, if necessary, by additional GC–mass spectrometry runs. The samples were quantified using ChemStation software (Agilent). Absolute amounts of neutral lipids were calculated as sum of fatty acids and fatty alcohols. For polar lipids, absolute amounts were not calculated. For the *Calanus* samples analysed at Unilab, an internal standard was not added prior to extraction and thus the fatty acids and fatty alcohols were presented as mass percentages of neutral and polar lipids separately. However, at Unilab, the sample dry matter (dried at 60°C for 24 h) and the total lipid extract from each sample were weighed, providing information on individual dry matter and total lipid content.

Samples for stable isotopes were prepared according to Søreide et al. (2006b), with removal of inorganic carbonates, and removal of lipids to reduce variability due to differences in lipid content. Stable isotope ratios were expressed in the conventional δ notation as the deviation from standards in ‰ according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000 \quad (1)$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. International standards, Pee Dee Belemnite for $\delta^{13}C$ (PDB: USGS 24), and atmospheric air for $\delta^{15}N$ (IAEA-N-1 and 2) were used to determine R_{standard}.

Statistics

Statistical tests were performed using the freeware *R*: *t* tests were used when comparing two independent groups. One-way ANOVA followed by the post hoc tests, Tukey's honestly significantly different (HSD) or unequal Tukey's HSD were used when comparing multiple groups with similar or unequal number of replicates per group, respectively. If the variance between independent groups was unequal (i.e. Levene's T test $P < 0.05$), we used the Mann–Whitney U test (MWU-test) and Kruskal–Wallis multiple comparisons of mean ranks for all groups (Siegel and Castellan 1988). The significance level was set to $P = 0.05$ in all tests.

Results

Ice algae

The ice algal assemblages developed from nearly invisible at the end of March into a thick layer in the lowermost 3 cm of the ice by 10 April. In the Amundsen Gulf, the chl *a* concentration in the bottom ice layer increased from 0.3 mg m^{-2} in mid-March to 10–20 mg m^{-2} at the end of April and beginning of May (Fig. 3). In the land-fast ice in Franklin Bay, even higher ice algal biomass was recorded in mid-May, varying from 28 mg m^{-2} up to 102 mg m^{-2} (Fig. 3). The ice algal community in Amundsen Gulf and Franklin Bay was dominated by pennate diatoms, namely *Navicula pelagica* and *Nitzschia frigida* (Table 2). Prior to 6 April, the ice algal biomass was too low for fatty acid analyses. The highest percentages of polyunsaturated fatty acids (PUFAs) were recorded in early April (24.5%) in the Amundsen Gulf and in May (24.7%) in Franklin Bay (Table 3). During the period from 6 to 29 April, there was a distinct increase in the amount of the monounsaturated fatty acid (MUFA) 16:1n7 (28–40%; Table 3). The proportions of PUFAs declined as the amount of the MUFA 16:1n7 increased (Table 3). Moderate amounts of PUFAs were recorded, especially EPA (7–10%), together with 18:4n3 (2–3%) and DHA (1–2%; Table 3).

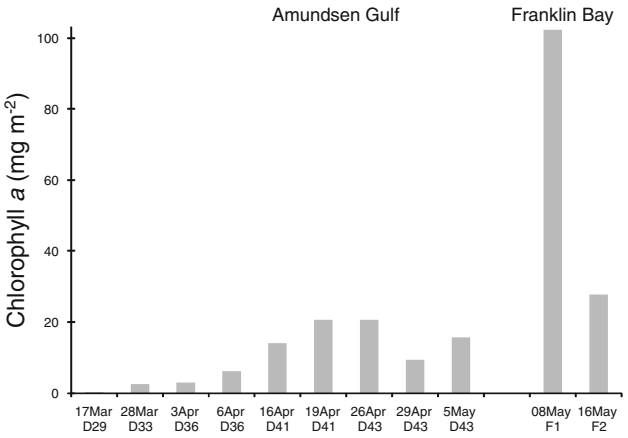

Fig. 3 Variation in the bottom ice chlorophyll (chl) *a* content (mg m^{-2}) in the Amundsen Gulf (March–May) and in Franklin Bay (May) in 2008

Calanus glacialis depth distribution and egg production

From January to April, the developmental stage CIII (55–68%) dominated the *Calanus glacialis* population, followed by CIV (23–37%; Fig. 4a). During May and June, CIV were the most numerous (55–60%), whereas in July more than 70% of the population consisted of CV (Fig. 4a). Females were present at all times, but with small contributions (<6%; Fig. 4a). Males were rare (<2%) and none were found in July. In June–July, the new generation (CI) started to appear and comprised <15% of the population in July (Fig. 4a). The total biomass of *C. glacialis* was relatively stable during the winter, ranging from 1.4 to 2.5 g DW m^{-2} and peaked in June at 3.8 g DW m^{-2} (Fig. 4b). The biomass was higher in the polynya than on the shelf, especially in June (Fig. 4b). Note that the proportions of smaller stages such as CIII contribute less when considering biomass than abundance and vice versa for the larger stages such as CV and females.

From January to March, the highest densities were found in intermediate layers (60–300 m, maximum bottom depth 350 m; Fig. 5). Already in March, CIV was recorded close to the surface, and from April, an abundance of AF, CV, CIV and CIII was located in the upper 100 m and close to the ice under surface. By May–June, most of the population was found in the upper 20 m (Fig. 5). In January, females were evenly distributed throughout the water column, but from March to June, females were mainly concentrated in the upper 60 m (Fig. 5). CIII and CIV were found at all depths from January to June, while CV was mainly concentrated in the surface layers (0–60 m) when they started to appear in high numbers in June (Fig. 5).

Table 3 Composition (mass%) of the four major fatty acids and the sums of polyunsaturated (PUFA), monounsaturated (MUFA) and saturated fatty acids (SAFA) of ice algae in the Amundsen Gulf (AG, April) and Franklin Bay (FB, May) in 2008

Date	06 April	11 April	16 April	29 April	08 May	16 May
Station	D36	D38	D41	D43	F1	F2
Area	AG ($n = 3$)	AG ($n = 3$)	AG ($n = 6$)	AG ($n = 6$)	FB ($n = 6$)	FB ($n = 3$)
16:1n7	27.5 ± 1.2	27.8 ± 1.9	35.8 ± 1.2	40.2 ± 0.8	34.1 ± 3.6	44.5 ± 0.2
18:4n3	2.5 ± 0.1	1.9 ± 0.1	1.8 ± 0.2	1.5 ± 0.3	1.5 ± 0.2	0.6 ± 0.1
20:5n3	10.1 ± 0.2	7.4 ± 0.6	8.6 ± 0.5	6.9 ± 0.9	10.7 ± 1.0	8.0 ± 0.2
22:6n3	1.8 ± 0.1	1.2 ± 0.0	1.0 ± 0.1	0.8 ± 0.1	2.8 ± 1.4	0.6 ± 0.0
∑ PUFA	24.5 ± 0.7	20.9 ± 1.3	20.4 ± 1.1	16.7 ± 1.5	24.7 ± 0.8	15.9 ± 0.3
∑ MUFA	31.5 ± 1.3	30.9 ± 1.8	38.4 ± 1.3	43.4 ± 0.8	40.6 ± 3.7	47.0 ± 0.3
∑ SAFA	44.0 ± 1.4	48.2 ± 3.0	41.2 ± 1.9	39.9 ± 1.9	34.7 ± 3.6	37.1 ± 0.6

Mean values ± standard deviation; n = number of replicates

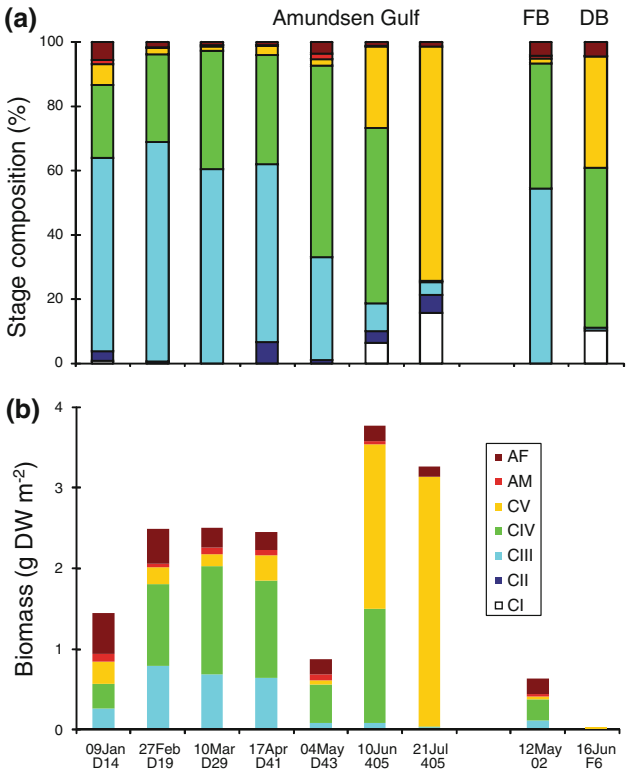

Fig. 4 Proportion (**a**) of the copepodid stage composition based on abundance data and biomass (**b**) of *Calanus glacialis* at different stations in the Amundsen Gulf (January–July), Franklin Bay (FB, May) and Darnley Bay (DB, June)

C. glacialis females started to spawn in the second week of April with a significant increase in the proportion of spawning females from early to mid-April (Table 4). The maximum egg production in Amundsen Gulf reached 28 eggs female^{-1} day^{-1} in early May. In Franklin Bay, egg production measurements were only taken on 11 May and females laid on average 36 eggs female^{-1} day^{-1}.

Calanus glacialis lipids

The amount of storage lipids, i.e. neutral lipids, decreased gradually during spring for *C. glacialis* females in the Amundsen Gulf (Fig. 6a). The highest amounts of neutral lipids were recorded in early February (413 µg ind.$^{-1}$) and the lowest amounts in May (94 µg ind.$^{-1}$). In July, the amount of neutral lipids increased again, and particularly high levels (454 µg ind.$^{-1}$) were recorded for *C. glacialis* CV (Fig. 6a). In Darnley Bay, females had relatively high neutral lipid weights in June, comparable to females in late February in the Amundsen Gulf (Fig. 6a).

For females, the relative fatty acid composition changed little during the winter–spring transition (February–May) in the Amundsen Gulf and Franklin Bay, but a slight increase in the percentage of PUFAs, from 9 to 14%, and a slight decrease in the percentage of MUFAs (e.g. de novo synthesized 20:1n9 and 22:1n11), from 72 to 63%, were seen from late March to May (Table 5). The main moieties of the neutral lipids during February–May were the diatom FATMs 16:1n7 (28–31%) and EPA (5–8%), as well as the typical *Calanus* de novo synthesized fatty acids 20:1n9 (9–20%) and 22:1n11 (7–13%), in addition to the SAFAs 14:0 (9–12%) and 16:0 (7–11%) (Table 5; Fig. 6b).

In March and April, fatty acid composition of surface (0-50 m) and deep-dwelling (200–450 m) females was also available (Table 5). In March, surface and deep-dwelling females had similar fatty acid composition, whereas in April, females at depth had distinctly lower proportions of diatom FATMs (28% vs. 39%) and higher proportions of dinoflagellate and bacteria (only 1.8%) FATMs, as well as 18:1n9, than those in the surface (Table 5). In the Amundsen Gulf in summer (July), females and CV had similar fatty acid compositions, with particularly high proportions of diatom FATMs (>50%) mainly due to higher proportions of EPA and C16 PUFAs than found

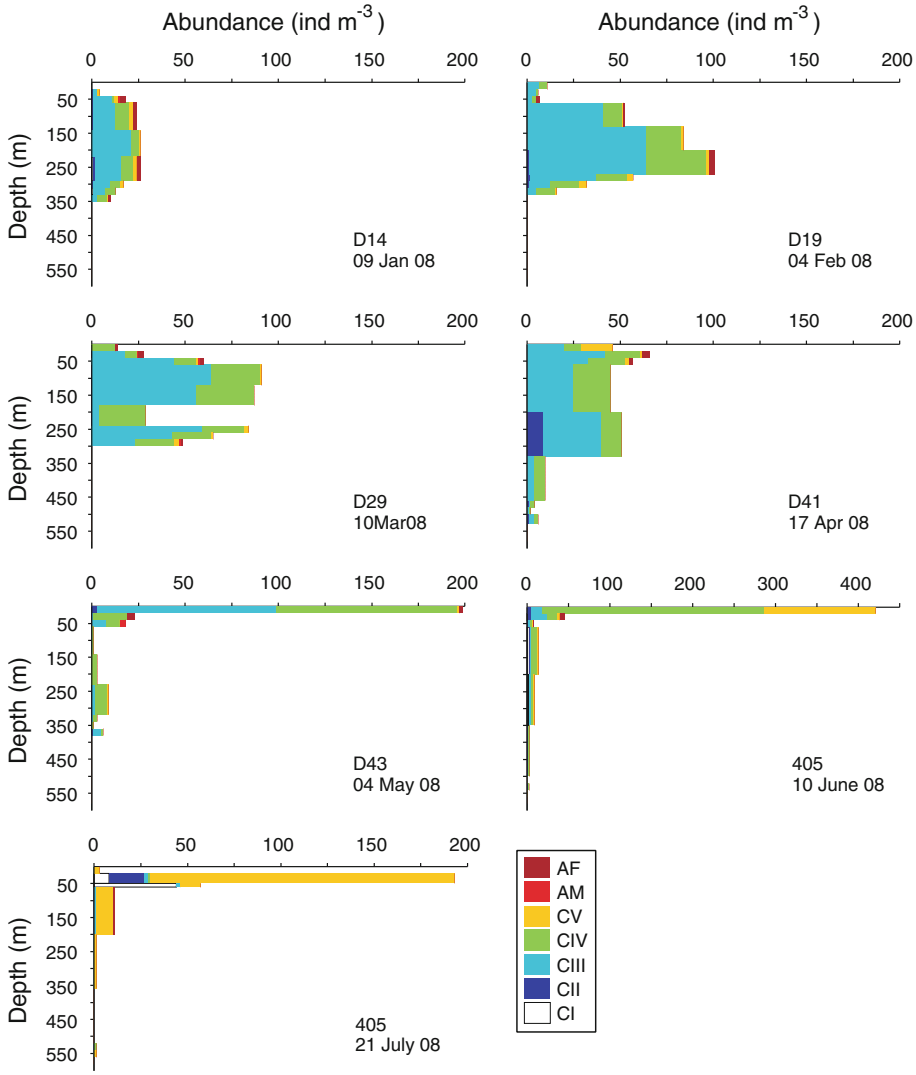

Fig. 5 Depth distribution in the abundance of *Calanus glacialis* copepodids in the Amundsen Gulf from January to June 2008

Table 4 Total number of females incubated (# females), spawning frequency (proportion of spawning females), egg production rates (EPR; the number of eggs female^{-1} day^{-1}) and clutch size as mean of the 3-day incubation for Amundsen Gulf (AG) and Franklin Bay (FB) during spring 2008

Date	Area	Stn.	# Females	Spawning frequency	EPR (eggs fem^{-1} d^{-1})	Clutch size
18 March	AG	D29	26	0	0	0
24–27 March	AG	D33	20	0	0[a]	0
1–3 April	AG	D33	20	0	0[a]	0
8 April	AG	D36	30	0.5	26.4	92.2 ± 38.5
8–11 April	AG	D36	20	0.5	7.5[a]	45.2 ± 15.2
12–15 April	AG	D36	20	0.6	11.7[a]	58.3 ± 25.0
16 April	AG	D41	30	0	0	0
26 April	AG	D43	30	0	0	0
2 May	AG	D43	10	0.1	1.5	15.0 ± 0.0
2 May	AG	D43	28	0.5	28.1	52.5 ± 23.8
19 May	AG	405	30	0	0	0
11 May	FB	02	28	0.4	36.3	84.5 ± 0.0

[a] Number of eggs female^{-1} day^{-1} as mean of 3-day incubation

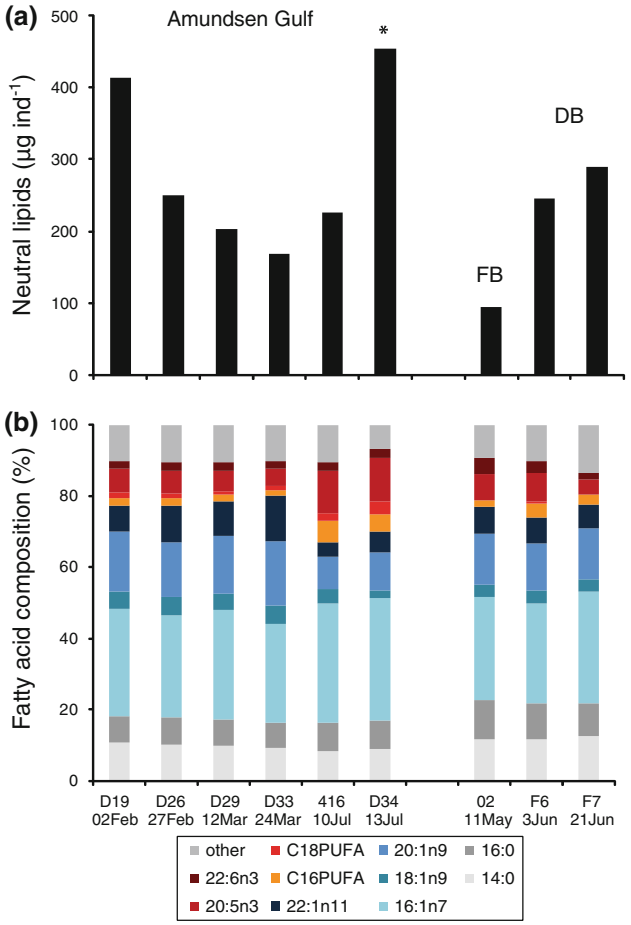

Fig. 6 The absolute amount of neutral lipids (**a**) and the relative fatty acid composition (**b**) in *C. glacialis* females in the Amundsen Gulf (February–July) and in Darnley Bay (June) in 2008; data from July 13 (*asterisk*) are for *C. glacialis* CV

during winter–spring (Table 5; Fig. 6b). The proportions of the MUFAs 20:1n9 and 22:1n11 were relatively low in summer versus the winter–spring period (Table 5; Fig. 6b).

The fatty alcohol composition of females did not change much during the winter–spring transition, with dominance of the fatty alcohols 20:1n9 (40–46%) and 22:1n11 (29–34%, Table 5). In summer (July), the proportions of the fatty alcohols 20:1n9 was rather low (33%) compared to winter–spring (Table 5). The fatty acid and fatty alcohol composition of females from Darnley Bay in June was similar to those of females from the Amundsen Gulf in May (Table 5).

For CIV, the same fatty acids and fatty alcohols as for females dominated, but the 20:1 and 22:1 fatty acids (13.4%) and fatty alcohols (66–69%) comprised a lower proportion of the neutral lipids for CIV than for females (Table 5).

For females, the polar lipids were dominated by the SAFAs, 16:0 (14–30%) and 18:0 (6–16%), and the PUFAs, EPA (4–18%) and DHA (3–23%; Table 6). The percentages of DHA were relatively low in February–March, and in individuals collected at depth in April (3–11%), compared to females collected in late March–April (19–23%; Table 6). In early April, females in the surface layer had higher amounts of EPA (4% vs. 13%) and DHA (3% vs. 19%) than females collected at depth (Table 6).

Calanus glacialis stable isotopes

No differences in δ^{13}C and δ^{15}N values were found for females in the surface and deep layer in March, so these samples were pooled (*t* tests, $P > 0.93$). During March and April, similarly enriched δ^{13}C values were found for *C. glacialis* females (one-way ANOVA, $P = 0.53$; Fig. 7). Similarly high values of δ^{15}N were found for females in March and the first week of April (mean 11.5‰; *t* test, $P = 0.17$), whereas in the second week of April, females were slightly less enriched in ^{15}N (mean 10.7‰; one-way ANOVA, $P = 0.04$; Fig. 7). In March, *C. glacialis* CV were slightly more enriched in ^{13}C than the females (*t* test, $P = 0.04$), whereas their δ^{15}N values were similarly high (*t* test, $P = 0.51$; Fig. 7). No differences in δ^{13}C (*t* test, $P = 0.15$) nor δ^{15}N (*t* test, $P = 0.39$) values were found for *C. glacialis* CIV in the first and second week of April, so these samples were pooled (Fig. 7). *C. glacialis* CIV had particularly low δ^{15}N values (mean 8.7‰) compared to females and CV (Fig. 7).

Stable isotope data on particulate organic material from the bottom of the sea ice (Ice-POM) and from the chl *a* max in the water column (P-POM), data from Forest et al. (2011) taken during the same cruise, showed that the δ^{13}C values of *C. glacialis* during spring (March–April) were more similar to those found for Ice-POM than P-POM (Fig. 7). The mean spring stable isotope value for *C. glacialis* reported by Forest et al. (2011) from the same survey (also included in Fig. 7) is difficult to compare to our results because they pooled CIV, CV and females.

Discussion

Sea ice and primary production

Since winter–spring 2008 was characterized by unusually reduced ice cover and periods of anomalously warm surface temperatures (Barber et al. 2010), the CFL sampling campaign turned out to be highly relevant for studying potential effects of reduced ice cover on Arctic marine ecosystems in the south-east Beaufort Sea. The land-fast ice bridge that typically forms in the Amundsen Gulf in March–April did not consolidate that year, and a rapid break-up of the ice in that region occurred as soon as early May (Barber et al. 2010). Ice algae started to grow by the

Table 5 Composition (mass%) of major fatty acids and alcohols (mean ± standard deviation) of the neutral lipid fraction of *Calanus glacialis* females (AF), CV and CIV from Amundsen Gulf (AG, February–April and July), Franklin Bay (FB, May) and Darnley Bay (DB, June) in 2008

Bottom-surface										Distinct depths					
Date	02 February	27 February	12 March	24 March	11 May	03 June	21 June	10 July	13 July	24 March	25 March	08 April	16 April	25 March	16 April
Station	D19	D26	D29	D29	02	F6	F7	416	D34	D33	D33	D36	D41	D33	D41
Area	AG	AG	AG	AG	FB	DB	DB	AG	AG	AG	AG	AG	AG	AG	AG
Depth (m)	Bot-0	Bot-0	Bot-0	Bot-0	Bot-0	Bot-0	Bot-0	Bot-0	Bot-0	50-0	170-100	50-0	450-200	170-100	450-200
Stage	AF	AF	AF	AF	AF	AF	AF	AF	CV	AF	AF	AF	AF	CIV	CIV
N (Σ ind.)	1 (16)	1 (16)	1 (15)	1 (15)	1 (16)	1 (15)	1 (15)	1 (15)	1 (15)	2 (15)	3 (15)	2 (15)	1(15)	2 (25)	1 (25)
Fatty acids (%)															
14:0	10.8	10.3	9.9	9.1	11.7	11.7	12.6	8.4	9.0	8.3 ± 1.2	9.0 ± 0.3	9.9 ± 0.3	10.2	6.6 ± 0.3	9.1
16:0	7.2	7.6	7.2	7.2	11.0	10.2	9.2	7.8	7.8	5.7 ± 0.2	5.7 ± 0.3	4.8 ± 0.4	9.0	6.5 ± 1.0	9.0
16:1n7	30.5	28.7	31.1	27.8	28.9	28.0	31.5	33.7	34.7	30.1 ± 0.5	29.3 ± 1.2	29.6 ± 4.7	17.9	14.9 ± 1.2	19.0
18:0	0.8	1.0	0.6	0.7	0.9	0.9	0.8	0.9	0.6	0.9 ± 0.2	1.0 ± 0.1	0.8 ± 0.0	2.1	5.5 ± 0.5	2.4
C16 PUFA	2.2	2.0	1.9	1.4	1.7	4.0	2.8	5.9	4.8	2.6 ± 0.4	2.4 ± 0.3	2.2 ± 0.3	2.8	5.9 ± 0.5	5.8
18:1n9	4.9	5.1	4.4	5.0	3.5	3.5	3.2	4.0	2.1	3.9 ± 0.1	4.2 ± 0.4	3.7 ± 0.6	6.3	3.0 ± 0.0	3.8
18:1n7	1.3	1.5	1.4	1.5	2.0	1.6	1.8	1.6	1.0	1.0 ± 0.1	0.9 ± 0.1	1.0 ± 0.0	1.0	0.8 ± 0.1	0.8
C18 PUFA	1.4	1.4	1.2	1.2	0.0	0.7	0.0	2.2	3.6	4.4 ± 0.2	4.8 ± 0.3	3.6 ± 0.2	5.7	12.1 ± 0.9	6.1
20:1n9[a]	17.9	17.0	17.4	19.6	15.4	14.4	15.6	10.2	11.0	14.4 ± 0.1	12.9 ± 0.6	15.2 ± 2.5	15.3	6.9 ± 0.1	7.0
22:1n11	7.2	10.3	9.7	12.8	7.6	7.2	6.6	4.1	5.9	8.0 ± 0.5	8.0 ± 0.4	9.0 ± 1.5	7.1	5.3 ± 0.6	5.3
22:1n9[a]	2.2	2.6	2.6	2.8	1.9	2.2	2.4	1.9	1.2	2.1 ± 0.2	1.7 ± 0.2	2.0 ± 0.1	1.6	1.3 ± 0.3	1.1
20:5n3 (EPA)	6.8	6.3	5.6	4.9	7.5	7.9	4.2	12.0	12.2	7.0 ± 0.3	7.9 ± 1.8	7.3 ± 0.4	7.7	14.8 ± 1.2	17.6
24:1n9	1.7	1.7	1.6	1.5	2.0	1.9	4.4	2.1	1.0	0.6 ± 0.1	0.5 ± 0.1	0.6 ± 0.0	0.6	0.4 ± 0.0	0.4
22:6n3 (DHA)	2.0	2.6	2.4	2.0	4.5	3.6	1.9	2.3	2.4	0.9 ± 0.2	0.8 ± 0.2	0.8 ± 0.1	1.4	1.0 ± 0.1	1.3
Others	3.2	1.9	3.1	2.3	1.3	2.2	3.0	2.9	2.6	9.7 ± 0.0	10.4 ± 0.6	9.6 ± 0.1	11.3	14.5 ± 1.8	11.2
FATMs (%)															
Diatoms	39.5	37.0	38.5	34.1	38.2	39.9	38.5	51.7	51.7	39.7 ± 0.2	39.6 ± 1.1	39.0 ± 5.4	28.4	35.5 ± 1.9	42.3
Dinoflagellates	3.3	4.1	3.6	3.2	4.5	4.3	1.9	4.6	6.0	9.3 ± 0.1	10.4 ± 0.1	8.5 ± 0.4	10.3	17.9 ± 0.4	10.6
Bacteria	1.5	0.6	1.3	1.0	0.0	0.7	1.6	1.2	0.8	1.1 ± 0.1	1.1 ± 0.0	0.9 ± 0.1	1.8	4.2 ± 0.8	2.0
Calanus	27.3	29.9	29.7	35.2	24.8	23.8	24.6	16.2	18.1	24.5 ± 0.6	22.6 ± 1.1	26.3 ± 4.0	24.0	13.4 ± 0.3	13.4
Sum (%)															
PUFA	12.7	12.4	11.4	9.5	13.8	16.2	8.9	22.6	23.5	19.8 ± 0.7	21.8 ± 1.9	19.1 ± 0.2	22.8	40.8 ± 0.9	36.2
MUFA	66.4	67.5	69.1	71.7	62.5	59.7	66.3	58.5	57.7	61.9 ± 0.1	59.5 ± 2.2	62.5 ± 0.1	51.5	35.0 ± 0.1	39.1
SAFA	21.0	20.1	19.5	18.7	23.7	24.1	24.8	18.9	18.6	18.3 ± 0.8	18.7 ± 0.5	18.4 ± 0.3	25.7	24.1 ± 1.0	24.6
Fatty alcohols (%)															
14:0	4.6	4.9	3.6	4.3	2.5	3.0	3.3	7.3	3.9	2.7 ± 0.1	3.2 ± 0.4	2.8 ± 0.1	2.7	6.1 ± 0.0	6.9
16:0	10.3	11.2	9.9	10.7	7.9	9.2	10.3	12.2	12.2	9.6 ± 0.7	10.4 ± 0.6	8.8 ± 0.5	9.0	12.9 ± 0.3	14.4

Table 5 continued

Bottom-surface										Distinct depths								
Date	02 February	27 February	12 March	24 March	11 May	03 June	21 June	10 July	13 July	24 March	25 March	08 April	16 April	25 March	16 April
Station	D19	D26	D29	D29	02	F6	F7	416	D34	D33	D33	D36	D41	D33	D41
Area	AG	AG	AG	AG	FB	DB	DB	AG	AG	AG	AG	AG	AG	AG	AG
Depth (m)	Bot-0	Bot-0	Bot-0	Bot-0	Bot-0	Bot-0	Bot-0	Bot-0	Bot-0	50-0	170-100	50-0	450-200	170-100	450-200
Stage	AF	AF	AF	AF	AF	AF	AF	AF	CV	AF	AF	AF	AF	CIV	CIV
N (Σ ind.)	1 (16)	1 (16)	1 (15)	1 (15)	1 (16)	1 (15)	1 (15)	1 (15)	1 (15)	2 (15)	3 (15)	2 (15)	1(15)	2 (25)	1 (25)
16:1n7	6.1	6.9	6.3	6.4	5.0	6.4	7.1	10.2	11.6	7.2 ± 0.7	10.0 ± 2.0	9.6 ± 2.0	4.5	9.6 ± 0.4	10.3
18:1n9[a]	4.8	5.0	4.5	4.5	4.2	4.5	4.9	5.4	4.2	3.4 ± 0.2	3.4 ± 0.0	3.4 ± 0.6	2.5	2.8 ± 0.2	0.0
20:1n9[a]	45.1	40.1	42.2	42.8	46.1	42.6	42.4	36.9	40.4	43.1 ± 0.0	42.8 ± 2.5	44.5 ± 0.8	49.1	33.4 ± 0.2	31.6
22:1n11	29.2	31.9	33.5	31.3	34.3	34.3	31.9	28.1	27.7	33.9 ± 1.7	30.2 ± 0.7	30.9 ± 2.5	32.2	35.3 ± 0.0	34.3

The sums of polyunsaturated (PUFA), monounsaturated (MUFA) and saturated fatty acids (SAFA) and the main fatty acid trophic markers (FATMs) are also included

[a] Includes minor % of the n7 isomer

end of March and peaked in mid-April. The early onset of the ice melt in May, however, terminated the ice algal growth season 1 month earlier compared to preceding years (Galley et al. 2008). By contrast, the fast ice and ice algae growth season in Franklin Bay and Darnley Bay most likely peaked in early May and continued until mid-June (Mundy et al. 2009). In these coastal areas, the ice cover duration was equivalent to previous years (Tremblay et al. 2008). In Amundsen Gulf, a first short phytoplankton bloom occurred in mid-May and was followed by relatively low chl *a* concentrations in June before a second less intense bloom was observed in mid-July (Forest et al. 2011). However, the chl *a* peak that was observed in mid-May may partly have been due to ice algal sedimentation (Fig. 3, e.g. (Tremblay et al. 2008). The strong contribution of ice-related pennate diatoms to these features early in the bloom season in May 2008 (Table 2) indicated that sea ice diatoms most likely had a significant share of the high pelagic algal biomass.

Life cycle and timing of reproduction

In the Amundsen Gulf, the *Calanus glacialis* population overwintered mainly as stages CIII and CIV in 2008, suggesting a 2- to 3-year life cycle. This observation is in contrast with previous studies from the Amundsen Gulf showing that CIV was the dominant overwintering stage in 2003–2004 during the Canadian Beaufort Sea Exchange Study (Makabe et al. 2010; G. Darnis, unpubl. data). In the eastern parts of the Arctic and western Greenland, the main overwintering stages of *C. glacialis* are CIV and CV, arguing for a 1- to 2-year life cycle there (Melle and Skjoldal 1998; Kosobokova and Hirche 2001; Madsen et al. 2001). The year 2007 was a special year in the Amundsen Gulf with regard to the record low ice cover (NSIDC 2011) and favourable winds for nutrient replenishment (Tremblay et al. 2006; Mundy et al. 2009). These conditions most likely resulted in a longer growth season for *C. glacialis* in 2007–2008 than in 2003, enabling CIV to develop to females that spawned late in the season (July) instead of having to overwinter as CIV and CV. The recruits of such an additional reproduction period late in the season of 2007 would have barely had the time to develop to CIII before diapausing. Such timing might explain the observation that CIII was the main overwintering stage in 2008. Ashjian et al. (2003) found *C. glacialis* to overwinter as a variety of stages in the western Arctic Ocean during the SHEBA annual cycle 1997–1998, including CIII and CIV. However, CIIIs were not as dominant in the overwintering populations as in the Amundsen Gulf in 2008. On the other hand, the extensive drift of the SHEBA project across different hydrographic regions and populations makes cohort development

Table 6 Composition (mass%) of major fatty acids (mean ± standard deviation) of the polar lipid fraction of *Calanus glacialis* females (AF) and CIV from Amundsen Gulf (AG) and Darnley Bay (DB) from January to July 2008

	Bottom surface				Distinct depth (females)					Distinct depth (CIV)			
Date	27 February	26 March	03 June	13 July	24–25 March		6–8 April		16 April	25 March	08 April	15–16 April	
Station	D26	D33	F6	D34	D33		D36		D41	D33	D36	D41	
Area	AG	AG	DB	AG	AG		AG		AG	AG	AG	AG	
Depth	Bot-0	Bot-0	Bot-0	Bot-0	50-0	170-100	50-0	270-200	450-200	170-100	50-0	50-0	450-200
Stage	AF	AF	AF	AF	AF	AF	AF	AF	AF	CIV	CIV	CIV	CIV
N (Σind.)	1 (15)	1 (15)	1 (15)	1 (15)	3 (15)	3 (15)	3 (15)	3 (15)	3 (15)	2 (25)	2 (25)	2 (25)	2 (25)
Fatty acids (%)													
14:0	1.7	1.5	2.0	4.0	6.3 ± 0.5	5.9 ± 0.4	5.4 ± 0.7	7.4 ± 0.4	5.5 ± 1.0	7.2 ± 0.5	6.5 ± 0.1	6.5 ± 0.2	6.4 ± 1.1
16:0	13.8	14.0	16.9	22.6	23.1 ± 0.3	21.5 ± 2.6	22.3 ± 1.3	29.8 ± 1.9	22.0 ± 5.8	32.2 ± 3.3	28.8 ± 1.4	23.9 ± 1.6	28.7 ± 2.1
16:1n7[a]	8.5	9.8	6.9	8.5	14.3 ± 1.4	16.0 ± 0.4	9.1 ± 1.7	6.8 ± 1.3	9.2 ± 2.9	9.7 ± 4.3	13.1 ± 1.5	8.2 ± 0.6	6.8 ± 0.4
C16 PUFA	1.2	1.3	1.3	1.4	2.1 ± 0.4	3.3 ± 0.8	1.2 ± 0.0	2.3 ± 0.5	1.4 ± 0.1	3.8 ± 1.7	4.7 ± 0.4	2.3 ± 0.0	1.7 ± 0.1
18:0	16.0	10.9	11.2	7.4	6.1 ± 1.6	6.0 ± 1.4	5.5 ± 0.6	16.3 ± 4.2	6.9 ± 3.9	12.9 ± 2.1	10.9 ± 0.6	10.4 ± 1.1	12.6 ± 1.0
18:1n9	6.9	5.8	3.0	1.8	5.2 ± 0.3	5.1 ± 0.8	3.6 ± 0.1	4.9 ± 1.1	5.1 ± 0.9	6.9 ± 2.4	8.4 ± 0.4	5.6 ± 0.7	4.8 ± 1.0
18:1n7	6.1	7.5	11.7	5.2	1.8 ± 0.3	1.5 ± 0.3	2.1 ± 0.1	0.9 ± 0.1	1.9 ± 0.8	0.8 ± 0.0	1.0 ± 0.1	1.2 ± 0.1	1.0 ± 0.1
C18 PUFA	4.6	2.0	1.4	1.9	2.9 ± 0.1	3.3 ± 0.2	3.1 ± 0.1	5.9 ± 1.1	4.2 ± 1.3	4.7 ± 1.1	5.2 ± 0.1	6.8 ± 0.9	6.2 ± 1.6
20:1n9	6.6	4.1	1.6	1.9	3.8 ± 0.6	3.3 ± 0.2	3.5 ± 0.2	1.0 ± 0.4	4.2 ± 2.5	0.5 ± 0.1	0.9 ± 0.0	1.3 ± 0.6	1.0 ± 0.2
20:1n7	1.2	0.7	0.4	0.2	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.1	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
20:4n3	2.4	1.5	0.0	0.3	0.1 ± 0.0	0.2 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0.5 ± 0.0	0.2 ± 0.1	0.6 ± 0.1	0.6 ± 0.0	0.5 ± 0.1
22:1n11	3.4	2.5	0.0	1.0	1.8 ± 0.4	1.8 ± 1.8	0.5 ± 0.0	0.6 ± 0.1	2.2 ± 1.5	0.4 ± 0.1	1.6 ± 0.3	0.8 ± 0.5	0.5 ± 0.1
22:1n9	1.7	1.2	0.0	2.5	2.0 ± 1.4	3.0 ± 0.4	1.5 ± 0.1	0.4 ± 0.2	1.9 ± 0.5	3.2 ± 0.8	0.3 ± 0.0	3.9 ± 1.8	3.8 ± 1.8
22:1n7	0.7	0.6	0.0	1.3	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.2 ± 0.1	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	0.3 ± 0.1
20:5n3	13.2	16.4	17.2	18.2	7.9 ± 1.8	7.7 ± 0.8	13.4 ± 1.8	3.9 ± 0.7	9.6 ± 2.8	2.8 ± 1.1	3.7 ± 0.3	8.0 ± 2.2	5.8 ± 0.5
22:5n3	1.1	0.2	1.8	1.6	0.3 ± 0.0	0.3 ± 0.0	0.5 ± 0.1	0.5 ± 0.1	0.6 ± 0.2	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.5 ± 0.1
22:6n3	10.8	18.7	22.6	18.5	11.4 ± 3.5	10.4 ± 1.3	18.6 ± 3.1	2.9 ± 0.5	15.2 ± 6.5	2.6 ± 1.3	3.2 ± 0.3	7.9 ± 3.7	6.0 ± 1.2
Other	0.3	0.2	0.3	0.3	10.7 ± 1.9	10.4 ± 0.6	9.2 ± 1.0	15.5 ± 0.5	9.2 ± 4.4	11.4 ± 0.1	10.6 ± 0.5	11.8 ± 1.2	13.1 ± 1.3
Sums (%)													
PUFA	33.2	40.0	44.3	41.8	28.7 ± 3.9	29.2 ± 2.7	40.6 ± 4.8	18.1 ± 2.3	32.9 ± 6.7	16.3 ± 3.3	19.5 ± 1.2	27.7 ± 4.8	23.2 ± 0.1
MUFA	35.1	32.2	23.6	22.4	31.0 ± 3.0	32.3 ± 2.9	21.5 ± 1.6	16.9 ± 3.1	26.8 ± 8.1	22.8 ± 2.9	26.5 ± 0.7	22.7 ± 0.5	19.7 ± 3.4
SAFA	31.8	26.6	30.5	34.3	40.3 ± 1.7	38.6 ± 5.4	37.9 ± 3.1	65.0 ± 5.4	40.3 ± 14.5	60.8 ± 6.2	54.0 ± 1.8	49.5 ± 4.3	57.1 ± 3.4

The sums of polyunsaturated (PUFA), monounsaturated (MUFA) and saturated fatty acids (SAFA) are also included

[a] Includes minor % of the n9 isomer

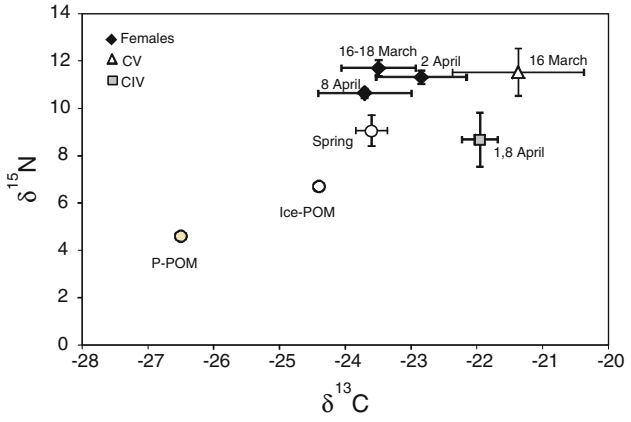

Fig. 7 Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope composition (mean ± SD) of *C. glacialis* females (16–18 March, 2 April and 8 April), CV (16 March) and CIV (1 April and 8 April) in the Amundsen Gulf during spring 2008. Stable carbon and nitrogen values of particulate organic matter from the bottom of the sea ice (Ice-POM) in mid-April and from the chl *a* max (P-POM) in mid-May as well average values of *C. glacialis* CIV-AF from spring (*spring*) are approximate values obtained from Forest et al. (2011)

analysis troublesome for the *Calanus* species. *C. glacialis* can overwinter as CIII, CIV and CV depending on the lipid content, but CIV and CV are the main overwintering stages (Madsen et al. 2001; Falk-Petersen et al. 2007, 2009).

The new generation in terms of CI and CII contributed little to the total *C. glacialis* copepodids in June–July in the Amundsen Gulf, suggesting that the recruitment from the April–May egg production was relatively weak. The small recruitment was likely due to the low abundance of CV and females during winter and hence few reproducing females in spring. However, the overwintering CIV (and maybe CIII) seemed to develop to CV during spring, and most likely to females that were able to spawn in late July/early August (see above). A second reproduction period in July/August is also indicated by the very high numbers of *C. glacialis* females found right underneath the ice in Franklin Bay in July (Hop et al. this volume) as well as observations of egg-producing females until mid-July in the same area (G. Darnis, unpubl. data). The relatively high occurrence of CI in Amundsen Gulf by early August 2008 (Forest et al. 2011) is further evidence that the July eggs rather than the April–May eggs contributed to the population recruitment in 2008. On the Canadian Beaufort Shelf (CBS) nearby the Amundsen Gulf, *C. glacialis* CI and CII made up close to 90% of the *C. glacialis* copepodids in early summer 2008. This indicates a high reproductive success in this area, explained by favourable food conditions as a result of early sea ice retreat and wind-induced upwelling of nutrients to the euphotic zone in 2007 and 2008 (Tremblay pers comm.). High primary production, due to mixing of nutrient-rich Pacific water at the shelf and hence high reproductive success of *C. glacialis*, is in accordance with the situation described at the Chukchi-Beaufort shelf region in 2002 (Plourde et al. 2005; Lane et al. 2008). In the Cape Bathurst polynya within Amundsen Gulf, an early ice melt was observed in spring 2008, but similarly high proportions of CI and CII such as those found for the *C. glacialis* population on the CBS in 2008 were not observed. A combination of overall lower food availability due to a reduced sea ice algal growth period, a subsequent brief and precocious phytoplankton bloom followed by a reduced pelagic primary production in June may have caused a potential mismatch between egg production and naupliar development and the algal blooms in the polynya (e.g. Søreide et al. 2010). Another potential explanation for the overall weak recruitment may be the low abundance of females. The poor contribution of females to the population (~4%) during spring contrasts with findings from other areas, e.g. East and West Greenland (Hirche et al. 1994; Hirche and Kwasniewski 1997; Madsen et al. 2001), the Laptev Sea (Kosobokova and Hirche 2001), the White Sea (Kosobokova 1999), the Barents Sea (Melle and Skjoldal 1998; Hirche and Kosobokova 2003; Wassmann et al. 2006) and the Svalbard region (Søreide et al. 2008, 2010). However, the total biomass of *C. glacialis* in Amundsen Gulf and the adjacent shelf areas was similar to that reported for the above-mentioned areas, except for the particularly high biomasses of *C. glacialis* in Hinlopen (26 g DW m^{-2}) and Rijpfjorden (31 g DW m^{-2}) in northern Svalbard (Søreide et al. 2008). In 2008, the peak biomass of *C. glacialis* in the Amundsen Gulf occurred in July (3.8 g DW m^{-2}). In the Amundsen Gulf, a possible second period of reproduction in July may have led biomass to peak later in fall. We do not have data from fall to confirm this possibility, but during the CASES study of 2004, the *C. glacialis* biomass maximum was reached in August in Franklin Bay (Forest et al. 2008).

Egg production and storage lipids

In the Amundsen Gulf, *C. glacialis* started to ascend to the surface in March, by April a large part of the population was recorded in the upper 60 m and most of the copepods were located in the surface by May. Females started to spawn in April after the onset of the ice algal growth season, with the highest egg production rates coinciding with the peak of ice algal biomass from mid-April to May. Females normally use ~14 days to mature when food is available (Hirche and Bohrer 1987), a delay that fits well with the time lag between the onset of the ice algal growth and the egg production. The marked decrease in storage lipids of females from February to May (Fig. 6a) coincided with the significant decrease in C:N ratio for *C. glacialis*

measured by Forest et al. (2011), and both results confirm the use of internal lipids during spring. The reduction in storage lipids for females during February–March was most likely related to higher energy demand after diapause (Seuthe et al. 2007), and particularly for the energy-demanding gonad maturation (Hirche and Kattner 1993; Jonasdottir 1999). Despite access to ice algal food in April, the amounts of neutral lipids in females continued to decrease until May. During the winter–spring transition in Franklin Bay, the same pattern of reduction of females' lipid reserves occurred in 2004 despite active feeding (Seuthe et al. 2007). Previous feeding experiments with *C. glacialis* during egg production showed that the females can utilize half of their lipid reserves during gonad maturation and thus will need the input of extra energy to fuel high egg production (Hirche and Kattner 1993). Not until July, during the second peak in phytoplankton biomass, did females in the Amundsen Gulf start to regain lipids. However, whether these females had been reproducing during spring or whether they had newly developed from CV remains unknown.

The low to modest egg production rates (EPR) in April–May in Amundsen Gulf were comparable to those found during early bloom phases in the Barents Sea (Melle and Skjoldal 1998), northern Svalbard (Leu et al. 2011), Greenland Sea (Hirche et al. 1994; Hirche and Kwasniewski 1997), central Laptev Sea (Kosobokova and Hirche 2001), Resolute Passage (Conover and Huntley 1991), and Chuckchi and Beaufort Sea (Plourde et al. 2005). Large variability in EPR was, however, observed for the 24-h incubations in April–May (0–28 eggs female^{-1} day^{-1}). This may be related to the many immature females observed on 16 and 26 April and 19 May. The clutch sizes in our study were comparable to average clutch sizes reported from the Chuckchi and Beaufort Sea in the spring (Plourde et al. 2005) as well as from other areas in the Arctic (Hirche and Bohrer 1987; Kosobokova and Hirche 2001; Madsen et al. 2008). Furthermore, the range of spawning frequencies within the Amundsen Gulf (0.1–0.6, when excluding the special stations where no egg production occurred) was close to what Plourde et al. (2005) found across the shelf-basin boundaries from the Chukchi/Beaufort Sea to the Canada Basin (0.2–0.6). The clutch size and spawning frequency can decrease substantially during food scarcity (Hirche and Bohrer 1987; Hirche 1989), although relatively high clutch sizes have also been reported for starving females (Kosobokova and Hirche 2001). However, the effect of starvation is very dependent on the female's condition at the time of capture, i.e. whether collected prior, during or after the peak bloom period (e.g. Kosobokova and Hirche 2001; Madsen et al. 2008).

Calanus glacialis fatty acid and stable isotope composition

The high neutral lipid content and the high proportion of the energy-rich long-chain 20:1 and 22:1 fatty acids and fatty alcohols in *C. glacialis* females in February suggest a low utilization of lipids during diapause, which has also been proposed by others (Hagen and Auel 2001; Lee et al. 2006). These energy reserves were likely used for the energy-demanding processes of gonad maturation and reproduction as illustrated by the spring decrease in females' lipid content. The essential fatty acids EPA and DHA constituted a larger part of the polar lipid fraction in females than in CIV, indicating that these fatty acids, needed for egg production (Sargent and Falk-Petersen 1988), were selectively retained by the females. Even though the females were actively grazing on ice algae during the bloom in April, the proportion of EPA and DHA decreased, as a further indication that they were used for egg production. The relative decline in the fatty acids and fatty alcohols 20:1 and 22:1 and the relative increase in PUFAs in the females during the winter–spring transition in Amundsen Gulf support the utilization of fresh algae. Previous studies from the same region also confirm that *C. glacialis* females actively feed during the winter–spring transition, as shown by the increasing faecal production as the spring progressed (Seuthe et al. 2007).

C. glacialis females in the Amundsen Gulf and nearby coastal areas were utilizing both the ice algal and water column diatoms early in the season as reflected by their fatty acid composition. The contribution of diatom FATMs was important in *C. glacialis* females throughout the season, but increased from March to May and peaked in July. The dominance of diatoms in the ice algae was also confirmed by taxonomical analyses of ice algae in this study (Table 2) and earlier ones (Michel et al. 2006; Juul-Pedersen et al. 2010). Compared to the European Arctic, the western Canadian Arctic has much higher silicate concentrations, due to the influence of silicate-rich Pacific water. The western Canadian Arctic is therefore able to support a higher diatom production than the European Arctic, which can explain the dominance of diatom FATMs in *C. glacialis* throughout the year in the Amundsen Gulf. In the European Arctic, the much larger variation in dietary fatty acid composition reflects the relatively large changes in the phytoplankton community composition during the productive season (e.g. Søreide et al. 2008).

Because all diatoms are characterized by high proportions of the MUFA, 16:1n7, C16 PUFAs and EPA, it is not possible to distinguish between a diet comprised of ice *versus* pelagic diatoms (Søreide et al. 2008). On the other hand, ice algae are more enriched in ^{13}C than phytoplankton, making it possible to trace ice algal versus

phytoplankton carbon sources by investigating $\delta^{13}C$ values of the consumers (Søreide et al. 2006a). In March and April, *C. glacialis* had $\delta^{13}C$ values closer to the C isotope signature of ice algae than phytoplankton. The decrease in $\delta^{15}N$ levels for females in April combined with increased proportions of C16 PUFAs and the MUFA 16:1n7 also suggest that *C. glacialis* fed on ice algae. Forest et al. (2011) reported lower $\delta^{13}C$ values for *C. glacialis* than what we observed from the same area and period. This discrepancy may be due to differences in methods, such as pooling CIV, CV and female *C. glacialis* prior to analyses. Furthermore, they did not remove lipids prior to stable isotope analyses but corrected for lipids (which are depleted in ^{13}C) afterwards, using the mass balance method of Smyntek et al. (2007).

Conclusions

A reduction in sea ice thickness and coverage as observed in the Amundsen Gulf in 2007 and 2008 can affect the timing of the reproduction of *Calanus glacialis*. In the south-eastern Beaufort Sea, *C. glacialis* overwintered mainly as CIII and to a lesser extent CIV, and few CV and females were present during winter and spring. This pattern is in contrast to what has been previously recorded from this same area in 2003–2004, and from the European Arctic where CIV and CV are the main overwintering stages. Despite the large amounts of ice algae available during the peak of egg production at the end of April, we observed low or very late recruitment of *C. glacialis* in the Amundsen Gulf in 2008. The reason for the possible mismatch between egg production/development could be either the early break-up of ice leading to a shorter ice algal bloom and an earlier phytoplankton bloom or the low numbers of CV and females during winter. The ice algae bloom in Amundsen Gulf in 2008 was likely more important for the development of *C. glacialis* CIII/CIV to CV and females than for supplying energy to egg production in early spring, a situation that differs from the European Arctic where females of *C. glacialis* utilized the high-quality ice algal bloom to fuel early maturation and reproduction (Søreide et al. 2010). The biomass of *C. glacialis* peaked in July, and the total biomass was comparable to other Arctic shelf areas (Madsen et al. 2001; Kosobokova and Hirche 2001; Hirche and Kosobokova 2003).

The high proportions of diatom FATM in *C. glacialis* females throughout the year suggest that diatoms are a more important food source for *C. glacialis* in the Amundsen Gulf than in the European Arctic seas. Enriched $\delta^{15}N$ values of females in the winter–spring transition suggest that females are opportunistic feeders during this period. As the spring progresses, their $\delta^{15}N$ values decrease as the input of fresh algae increases. Enhanced proportions of PUFAs during spring additionally confirm the increased intake of fresh algae.

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